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ON THE OCCURRENCE OF AN APUS IN THE PERMIAN OF OKLAHOMA

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Professor J. W. Beede last year sent two specimens of a crustacean from the Permian of Oklahoma to the New York State Museum for investigation. They were from a suite collected by Dr. Thomas T. Jackson in a thin sandstone bed of the Enid formation, exposed "on the top of a hill four or five miles north of Elkeno, Oklahoma."

The specimens[1] proved, on inspection, of exceptional interest for the reason that they not only exhibit an outline of the carapace as seen in Apus but even the impressions of the "shell-glands" or excretory organs in a form as it is today known in Apus, and its close relative Lepidurus. We have, therefore, no hesitation in considering this Permian form a true Apus, and propose for it the name *Apus beedei* sp. nov.

Apus beedei sp. nov.

Description.—Carapace small (the larger specimen 15 mm. × 14 mm.); broadly elliptic, nearly circular in outline, with a small posterior emargination; shieldlike and sloping from the subcentral apex abruptly forward, more gently backward, and probably originally fairly steeply toward the lateral margins. A transverse cervical fold is situated about one-fifth of the length of the carapace posterior to the anterior border. Immediately posterior to this are the large but slightly curved "shell-glands" or excretory organs; beginning at either side of the median line they extend obliquely backward about midway of the lateral faces of the carapace to about one-fifth of the length of the carapace from the posterior border. The median line is marked behind the cervical fold by a distinct depression extending about one-third of the distance toward the posterior border.

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[1] Professor Beede had stated in his letter that he had more specimens than the two sent but none showing features not seen in the ones inclosed. On inquiry, we learn that this further material is not available at present, but in view of Professor Beede's statement and the great interest of the material, we venture to publish this notice without having had access to the less favorably preserved specimens.

Horizon and locality.—Permian (Enid formation), near Elkeno, Okla.

Note on identification with Apus.—The writer is well aware that considering the enormous stretch of time from the Permian to the present time, and further the fact that only the carapace of the Permian form is now at hand, there is a great possibility that if the body of the animal were preserved, differences of generic importance might be quite apparent, e.g., such as now separate Lepidurus from Apus and which consist in the different development of the post-anal plate. It could, therefore, be urged that this Permian form should be made a separate genus on theoretic grounds. In such an attempt it would, however, be found that the carapace of the older form is not distinguishable from that of the recent type and the new genus would have no diagnosis, but only its great age to stand on. It is, however, to be understood

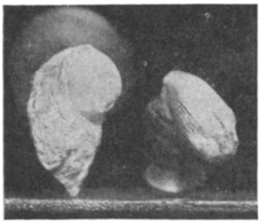

FIG. 1

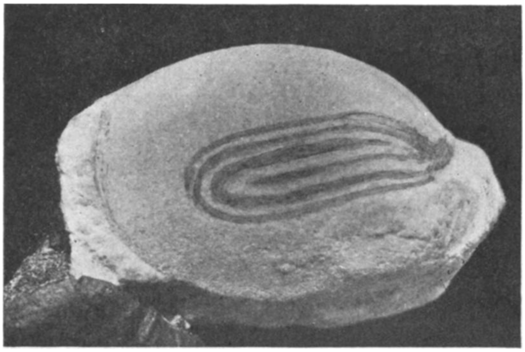

FIG. 2

FIG. 1.—*Apus beedei* sp. nov. The two specimens seen obliquely from above and the front. Natural size. The type-specimen is on the right. It shows the transversal wrinkle in the place of the cervical fold, portions of the frontal part of the carapace and the median depression.

FIG. 2.—*Apus beedei* sp. nov. Lateral view of the type-specimen. ×3. Shows the shell-gland and posterior emargination.

that the term Apus expresses here the hard parts only and the entire group (Apus and Lepidurus) and that it is merely intended to point out the persistence of the Apus-type of carapace. The persistence of the exact form of the carapace in the group indicates that no evolutionary development profound enough to affect the carapace took place in all this time.

Note on preservation of material.—The specimens are casts of the interior surface of the carapace. It is for this reason that the impressions of the shell-glands are so well preserved in some of the fossils, for it must be remembered that these organs are situated between the two layers that form the posterior portion of the carapace, and that these glands open where the inner layer terminates at the cervical fold. The frontal portion of the carapace is poorly preserved, partly no doubt on account of the greater thinness of the carapace there, which consists of but one layer, and partly owing to the lateral compression of the tests during entombment. There is, however, enough left of the frontal outline (especially in the smaller specimen) to leave no doubt that it was rounded and unbroken originally. It would seem that the shield was sufficiently sloping toward the lateral margins to come frequently to rest on the side and then suffer lateral compression. The amount of lateral slope is greater also in the recent Apus than the usual dorsal views of the creatures would suggest, as shown in the lateral view drawn from nature by the writer and reproduced in Figure 4. A restoration of the dorsal view of the carapace of *Apus beedei* is given in Figure 3. It is obtained by plotting the

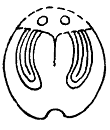

FIG. 3

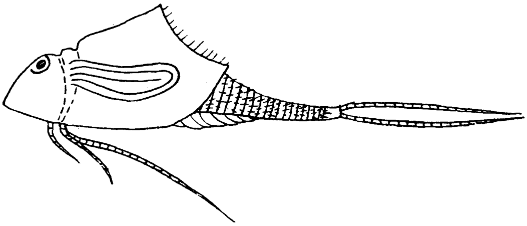

FIG. 4

FIG. 3.—*Apus beedei.* Flat projection of outline of carapace.

FIG. 4.—Lateral view of *Apus aequalis* Packard, ×2; from Colorado and in N.Y. State Museum.

larger specimen, in natural size, on the horizontal plane. An oblique view from above of the same specimen is given in Figure 1 and a lateral view in Figure 2. The former presence of a cervical fold in the Permian form, corresponding to that in recent species of Apus (Fig. 4, where it is shown in the profile behind the eye), is indicated by a transverse wrinkle, especially distinct in the larger specimen, but also seen in the smaller one. This wrinkle has resulted from the yielding of this transverse fold during lateral compression. It has thereby become pressed downward and changed into a deep transverse wrinkle, in front of which the carapace has split and been drawn inward. The smaller specimen retains the frontal portion in more perfect form, though also much compressed. Owing to this folding-in of the frontal part, the perforations of the carapace for the eyes are not observable.

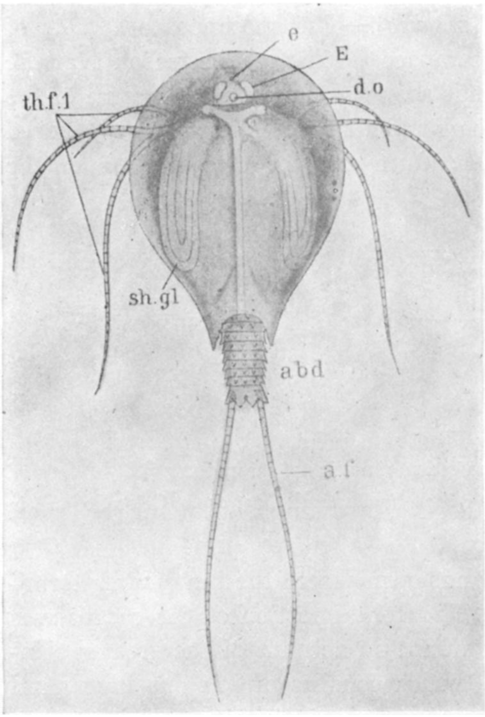

FIG. 5.—*Apus cancriformis* Schäffer. Dorsal aspect. From Parker and Haswell (after Bronn's Thierreich). *d.o.*, dorsal organ; *E*, paired eye; *e*, median eye; *sh. gl.*, shell-gland.

The shell-gland appears as an elongate elliptic body consisting of two concentric furrows and one median and another outer longitudinal one. There are thus altogether six urinary tubes counted on the transverse line, just as in the recent Apus (Fig. 5). All these are very distinct on both sides of the larger specimen and also well recognizable on the smaller one. They bend inward and downward at the cervical fold, where as in the recent form they open (at the underside of the body).

The median line of the carapace is marked in its anterior third behind the cervical fold by a deep depression, fading out backward, which corresponds to the carina seen in *Apus cancriformis* and some of its congeners.

The posterior emargination is distinct in both specimens though not appearing in the photographs. The original of Figure 2 is just sufficiently compressed obliquely to have the emargination transferred to the other side.

General bearing of discovery.—Apus has long been famous in paleontologic literature as a primitive phyllopod that on account of its great number of simple appendages and other primitive features has served well as a model for comparison with extinct crustaceans, especially with the trilobites; and again in the case of the wonderful middle Cambrian branchiopods discovered by Walcott in British Columbia. It is equally famous among zoölogists for its strange life-cycle as well as its archaic characters. Notwithstanding its frequent citation in paleontologic literature, a true Apus has only once been found in fossil state. This is the *Apus antiquus* Schimper from the Buntsandstein of the Vogesian mountains. This find carried the range of Apus back to the Triassic, and the occurrence in Oklahoma extends it now to the Permian.

Apus is thereby made one of the few persistent types that have existed from Paleozoic to recent time. Like Limulus it is a "living fossil." Connected with this amazing persistence is undoubtedly the strange life-cycle of this creature, as the writer will elaborate more fully in another paper. Apus, as typically represented by *Apus cancriformis*, appears only at long intervals, usually only after decades of years, during which the eggs were buried in the dry mud of roads, ditches, and desiccated pools and exposed to heat and cold. It is therefore an extremely rare animal and the writer still remembers with thrill, how when still a schoolboy he one day espied a large specimen crawling on the muddy bottom in the water of a swamp along which he was botanizing, rushed in, grabbed the strange creature, and ran back at top speed to the high-school professor of biology who promptly took it away declaring it to be the first he had ever seen alive! It is told of Goethe that he had one brought to him while walking once near Jena and that he became so excited over the weird animal that he offered a thaler for the second, a guilder for the third specimen, and so forth, but no other was found. *Apus cancriformis* grows within two weeks to full size which sometimes is nearly five inches, lays an enormous number of eggs and dies.[1] Another strange fact connected with this animal is that it produces the eggs parthenogenetically. It was fully a hundred years after the description of the species that any males were found. The seventy pairs of appendages (among them fifty-two pairs of abdominal feet with their gill-appendages) which give it its archaic appearance are also connected with its life in very temporary pools that lack the vegetation which oxygenates the water.

All these facts show that the animal is adapted to most peculiar, and it would seem also most precarious, conditions. It has been therefore thought by some, as Salter and Packard,[2] to be, together with the rest of the Branchiopoda, highly specialized and comparatively modern. Its fossil record, however, contradicts this conclusion, and from evidence, which the writer[3] in a former paper on arrested evolution has brought forward in regard to the factors of persistence in animals, it follows that Apus belongs to that class of persistent forms, that, at the height of their once vigorous development, were able to penetrate into fields where weaker forms could not follow them and it is precisely in these outskirts of the arena of organic struggle that these types, after they were overtaken by more rapidly developing forms, have managed to persist. This would suggest that Apus had followed its present mode of life through many periods, and the fossil evidence does not contradict this suggestion; for the single Apus found in the Buntsandstein may well have drifted in, together with the numerous remains of landplants (Voltzia, etc.) found in that Triassic terrane. Regarding the character of the Oklahoma deposit, from which our specimens came, Professor Beede writes me under date of December 14, 1921, that it might be brackish water or, possibly, even fresh.

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[1] Weigand, 1913.

[2] See Schuchert, 1897, p. 675.

[3] Ruedemann, 1918.

Leaving out the *Apus dubius* Prestwich, described from the Coal Measures of England, which, according to Beecher,[1] "seems to be an abdominal segment or plate of some eurypterid," there is evidence of a still older form, at least closely related to Apus, even in the Lower Cambrian. This is the well-known *Protocaris marshi* Walcott from the Waucoban (Georgian) of Georgia, Vermont. Its similarity to Apus was recognized by Walcott[2] and has since been commented upon by Clarke[3] and Bernard,[4] the latter author even proposing to call the form *Apus marshii.*[5] This Cambrian relative has also been found in but a single example and therefore was hardly a common marine form, as the tribolites collected in the same beds. Therefore, even this might have drifted in from the fresh water.

As to the remaining fossils that by some have been compared with Apodidae, we refer to Pompeckj's excellent summary in the chapter "Crustacea" in the *Handwörterbuch der Naturwissenschaften.*[6] The remarkable crustacean-fauna discovered by Walcott in Burgess-Pass contains both Notostraca (Burgessia and Naraoia) and Anostraca (as Opabinia, Leancholia, Yohoia), but not any forms that are directly referable to Apus, though some may, according to Pompeckj, be ancestral to later apodids, as Naraoia to the later Carboniferous Dipeltis, which behind the parabolic carapace possesses two large thoracic segments or rather shields.[7] The position of certain finds is considered doubtful, as that of a carapace, similar to Apus, described as *Lynceites ornatus* Goldberg from the Carboniferous of Saarbrücken and now currently referred to the Cladocera. There are further to be mentioned the problematic, laterally compressed carapaces of Ribeiria Sharpe and Ribeirella Schubert and Waagen, which occur in the Ordovician and Silurian of Bohemia, Portugal, England, and North America, and which were placed by Schubert and Waagen with the Apodidae and considered as possible ancestors of Apus. Pompeckj holds that neither this nor the leptostracan nature of these fossils can be proved. We believe that the two muscle-impressions which Ribeiria shows on the dorsal median-line[1] indicate that in this form the carapace was attached to the body in nearly its entire length along the dorsal line while in Apus it is free from the cervical fold backward, i.e., in its greater portion. This would already indicate a very different organism, even if the deep transversal sulcus in front of the apex of the casts of Ribeiria could in some way be compared with the cervical fold in the carapace of Apus.

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[1] See Schuchert, 1897, p. 675.

[2] 1884, p. 50

[3] 1893, p. 799.

[4] 1894, p. 413.

[5] Schuchert (1897, p. 674), however, points to the subquadrangular shield and frontal emargination as distinguishing characters.

[6] Pompeckj, 1912, p. 789.

[7] Schuchert, *op. cit.*

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[1] *Ribeiria compressa* Whitfield, *Bull. Amer. Mus. Nat. Hist. N.Y.*, Vol. I, No. 8 (1886), Pl. 33, Fig. 3.